Sensory Integration: Neuronal Filters for Polarized Light Patterns

Animal and human behaviour relies on local sensory signals that are often ambiguous. A new study shows how tuning neuronal responses to celestial cues helps locust navigation, demonstrating a common principle of sensory information processing: the use of matched filters.

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The eyes are a major gateway to the world. They enable us to recognize familiar faces, appreciate a beautiful landscape, or monitor how and where we move. But from an engineer's point of view the processes providing us with the full picture are often awfully complicated. The visual system does not have immediate access to sophisticated features, such as the face of a person. Photoreceptors in the eyes only measure changes of colour values and light levels on a pixel-by-pixel basis, which initially does not contain enough information to distinguish between different faces. A similar problem exists for animals that use their visual system to exploit celestial cues when keeping their heading relative to the sun — even in cloudy conditions. New research published in this issue of *Current Biology* [1] provides further insight into how specialized neurons in the locust brain allow the animals to navigate solely based on the pattern of polarized light in the sky.

All celestial cues locusts may use to control their heading depend essentially on the position of the sun. The most obvious one is the sun position itself, but this information might not be available if the sun is hidden behind some clouds. The good thing about the other cues is that they are useful even if only scattered patches of the sky are visible. One such cue is the light spectrum in the sky. The anti-solar hemisphere is dominated by the ultra-violet spectrum while light in the solar hemisphere assumes slightly longer wavelengths. We can see the difference when taking a photograph on a cloudless day. With the sun from behind the sky in the background will be deep blue. However, a picture taken against the sun will show a pale blue sky. Locusts may as well exploit such a chromatic gradient and the position of the sun [2] — if visible — but the cardinal cues they use for navigation depend on the animals' ability to sense linearly polarized light [3,4].

Linearly polarized light is a celestial cue tightly linked to the fact that light has the properties of an electromagnetic wave. It consists of an electric and a magnetic field oscillating in mutually perpendicular planes, both oriented orthogonally with respect to the travel direction of light. The orientation of the electric field is described by the e-vector. Sunlight is composed of a random mixture of e-vector orientations; but when it hits molecules in the atmosphere it becomes linearly polarized, which means that the e-vectors assume the same orientation. Both the degree of polarization — the fraction of light where the e-vectors oscillate in the same orientation — and the local orientation of the e-vector at different locations in the sky depend on the sun's position. Light at locations 90° away from the sun is maximally polarized. Minimum polarization occurs close to the sun and exactly opposite to its position. This fixed dependence on sun position allows us to calculate the entire distribution of local e-vector orientations in the sky, also called Rayleigh pattern (Figure 1A, blue double-headed arrows).

A necessary condition to exploit the Rayleigh pattern for navigation obviously requires the ability to measure e-vector orientation. Photoreceptors in the dorsal rim area of the locust eye are specialized for this job. The photo pigment mediating the transduction of light energy into neuronal signals is assembled in sub-compartments of photoreceptors called rhabdomeres. Membrane foldings of the rhabdomeres, or microvilli, are arranged in either of two perpendicular orientations along which they capture light. These structural specializations observed in several insect species enable an estimate of the local e-vector orientation based on the excitation levels of two photoreceptors with orthogonally arranged microvilli monitoring the same location in the sky [5]. In locusts, polarized light is only analysed by photoreceptors in the dorsal rim area that receive input from the upper visual hemisphere that features the Rayleigh pattern.

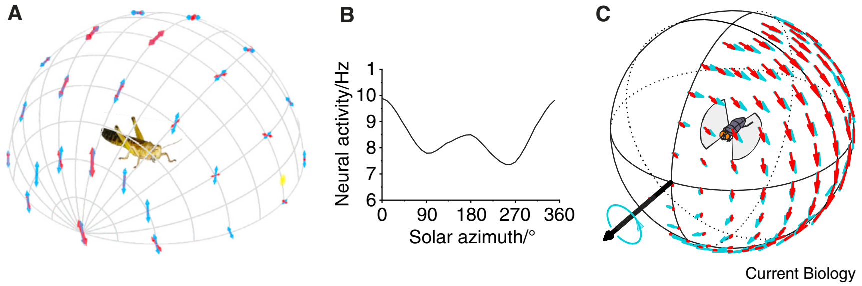

Figure 1. Matched filters for Rayleigh patterns and optic flow fields.

(A) The distribution of local e-vector preferences within the receptive field of a locust POL-neurons (red double-headed arrows) in the central complex matches the distribution of local e-vector orientations of a Rayleigh pattern (blue double-headed arrows). The neuron's receptive field comprises the entire upper visual hemisphere. The yellow dot indicates sun position. (B) Quantitative estimate of neural activity computed by spatially integrating the local dot products between the e-vectors of the Rayleigh pattern and the e-vector preferences of the POL-neuron as a function of solar azimuth. The resulting tuning curve shows a single maximum for a solar azimuth of 0° = 360°; i.e. when the sun is in front of the animal. (C) The distribution of local motion preferences (red arrows) within the receptive field of a motion-sensitive interneuron in the fly visual system matches the distribution of local velocity vectors (blue arrows) in an optic flow field induced in the left visual hemisphere during a clockwise roll-rotation of the animal. In both cases the selective spatial integration of local responses results in an increased specificity of the neurons for a particular Rayleigh pattern and an optic flow field, respectively. The outputs of such *matched filter* neurons may be used directly to control heading in locusts and stabilize flight in flies. (Data from [1,7].)

Knowing only the local e-vector orientation, however, does not provide the locust with unambiguous information about its body orientation relative to the sun. This is because one and the same e-vector orientation at a given location may result from two different positions of the sun separated by an azimuth of 180°. How does the visual system resolve this ambiguity?

Bech *et al.* [1] addressed this very question. They recorded the neural activities from polarization-sensitive neurons in locusts and compared the results with the known properties of Rayleigh patterns. As in previous studies, they stimulated the neurons with linearly polarized light the e-vector orientation of which was continuously changed while monitoring the responses. The neurons the authors focused on had been investigated before and are found in the central complex, a part of the insect brain likely to be involved in the control of locomotion. This time, however, when recording the activity of a single neuron the stimulus was only applied to a small area of <4° in diameter, but at 37 different locations within the upper visual hemisphere.

The results were remarkable in two respects. Firstly, these polarization-sensitive neurons had massively extended receptive fields — the area within which the changing e-vector orientation modulated the neuronal responses included the entire upper visual hemisphere. And secondly, the preferred e-vector of the studied neuron was not the same at the different stimulus locations, but changed systematically following the global structure of a specific Rayleigh pattern (Figure 1A, red double-headed arrows). Despite the demanding nature of their experiments, Bech *et al.* [1] were able to record from six neurons. They always found similar response properties confirming both the massive receptive field size and the location-dependent e-vector preferences [1].

The results suggested that the polarization-sensitive neurons spatially integrate a huge number of local signals each of which indicates a specific e-vector preference. By combining only those e-vector preferences which locally correspond to the e-vector orientation in a specific Rayleigh pattern the integrating neuron should be maximally activated only if the animal assumes a certain body orientation relative to the sun. Bench *et al.* [1] included a computational part in their study that supports this interpretation. Knowing the receptive field properties of a given neuron and the global structure of a Rayleigh pattern, the authors were able to calculate the neuronal activity as a function of sun position, or solar azimuth. The results calculated for one of the six neurons are plotted in Figure 1B. The calculated activity shows only one maximum. This suggests that, indeed, the output of the neuron could be used as an unambiguous signal to control the body orientation of the locust relative to the sun [1].

The new study [1] nicely demonstrates what appears to be a common principle in sensory information processing. In the late 1980s work on crickets and other insects exploiting polarized light for navigation inspired the idea that sensory systems use *matched filters* to extract specific stimulus patterns [6]. However, hard experimental evidence for this in terms of the underlying neuronal mechanisms has been sparse. Another example of matched filters being used to extract unambiguous visual information was presented for sensory-motor control in flies. In their third visual neuropile flies employ directional-selective neurons with expanded receptive fields matched to optic flow fields that are generated during self-motion in their visual surrounding [7]. The underlying mechanism is virtually the same as the one Bech *et al*. [1] found in locusts. In case of the fly, however, local directional motion preferences within the receptive field of a given neuron match the direction of local optic flow vectors at corresponding locations within the animal's visual field (Figure 1C, red and blue arrows). Each of those fly neurons was suggested to signal a specific body rotation [8] that may be caused by external perturbations such as gusts of wind.

The common theme in both polarization vision in locust and motion vision in flies seems to be that ambiguous local signals are spatially integrated in a task-specific way to provide robust signals for navigation and flight stability.

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Cell Cycle: Once Out, Never In Again

A recent study shows that prolonged inhibition of bacterial cell division causes a block of DNA replication, which is followed by an irreversible cell cycle arrest. The finding indicates a tight coupling between cell division and DNA replication in bacteria.

Kristina Jonas

Faithful progression through the cell cycle requires tight control of DNA replication, cell division and cellular growth. In eukaryotes, the cell cycle is divided into discrete phases, the G1, S, G2 phases and mitosis. Correct progression through these phases involves so-called checkpoints that